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THE
BOTANICAL GAZETTE

DECEMBER 1915

MASS MUTATION IN OENOTHERA PRATINCOLA¹

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(WITH FIFTEEN FIGURES)

Introduction

Of the several small-flowered wild evening primroses thus far examined by the writer for mutability, no other has yielded as valuable data as *Oenothera pratincola*. Certain mutations of this species have been treated in a former article,² of which this one is in effect a continuation. To recapitulate very briefly, it may be recalled that *O. pratincola*, a species found wild at Lexington, Kentucky, gives rise in successive generations to a small proportion of mutations, belonging to several distinct types. Of these the most conspicuous in the young condition is mut. *nummularia*, which originates in every generation from seven of the eight independent strains which have been studied. The eighth strain, designated in the former article as Lexington E, shows the phenomenon which the writer has elsewhere designated as mutation *en masse*.³ Mutant species in *Oenothera*, as typified by *O. Lamarckiana*, give rise to few mutations. The frequency of mutations in

¹ From the Bureau of Plant Industry, U.S. Department of Agriculture, Office of Plant Physiological and Fermentation Investigations. Published by permission of the Secretary of Agriculture.

² BARTLETT, H. H., Additional evidence of mutation in *Oenothera*. Bot. GAZ. 59:81-123. 1915.

³ ——, Mutation *en masse*. Amer. Nat. 49:129-139. 1915.

O. Lamarckiana is about 2 per cent. Some of its mutations are themselves mutable and give 4 per cent or even 6 per cent of secondary mutations.⁴ The ordinary strains of *O. pratincola* produce about 2 per cent of mutations,⁵ and the true *O. biennis*, of Holland, only about 0.45 per cent.⁶ In strains which show mass mutability, however, the number of mutations rises to 50 per cent or even 100 per cent. This is the case with Lexington E.

Lexington E differs from all the other strains of *O. pratincola* (1) in that it gives rise to a characteristic group of four mutations, (2) in that these characteristic mutations occur in such large numbers as to justify the use of the designation mass mutation for the phenomenon, and (3) in that it does not give rise to mut. *nummularia* and certain other mutations which are characteristically produced by the strains which do not show mass mutation.

Turning now to resemblances, we find absolutely no morphological characteristics to indicate even the slightest difference between Lexington E and the other strains of *O. pratincola*. Moreover, Lexington E shows also the ordinary type of mutability, in that it gives rise to small numbers of some of the same mutations which the other strains produce. These mutations are in no wise distinguishable morphologically from the same forms occurring in the other strains, but all the evidence at hand shows that when derived from the strain showing mass mutation the non-characteristic mutations themselves show mass mutability. The mutations characteristic of mass mutability are themselves mutable and throw as secondary mutations other members of the characteristic group.

In view of the extraordinary interest of the phenomenon of mass mutation, it is hoped that the reader will pardon the presentation of this confessedly preliminary report. Many of the genetic relationships between the mutations and the parent species remain to be worked out, and, as will be very obvious, a cytological study of the whole subject is imperative.

⁴ DEVRIES, H., Gruppenweise Artbildung. pp. 312-315.

⁵ An estimate based upon the results tabulated in BOT. GAZ. 59:105-109. 1915.

⁶ DEVRIES, H., The coefficient of mutability in *Oenothera biennis* L. BOT. GAZ. 59:169-196. 1915.

The characteristic mutations of the mass mutating strain

The four mutations, which by occurring in such large numbers characterize the hereditary behavior of Lexington E, form a group with a common structural peculiarity which sets them apart from typical *O. pratincola* and from all the other mutations. This peculiarity lies in the narrow, strongly revolute, veiny leaves, of which the midrib is frequently but not always prolonged from a point below the apex as a setiform appendage. This appendage strongly resembles the infra-terminal calyx tips of certain species of *Oenothera*, and suggests the translocation of a character from one organ to another which does not typically display it. The setiform appendage is exceptionally a centimeter long but is entirely absent on some leaves of each individual mutation. It may be said that the four mutations are characterized by the possibility of manifesting the appendage under favorable conditions rather than by its invariable presence. The revoluteness, narrowness, and venoseness of the leaves, however, are characters which are always distinctive.

The four characteristic mutations may be contrasted as follows:

Plants as tall as *O. pratincola* f. *typica*, with a much-branched terminal inflorescence; fruiting freely by self-pollination and producing a normal number of viable seeds.....mut. *formosa*

Plants semi-dwarf; leaves whitish, broader and thicker than in the last; inflorescence often simple and bearing a few thick-tissued, usually cleistogamous flowers; producing by self-pollination large, apparently normal capsules which contain very few seeds.....mut. *albicans*

Plants semi-dwarf; leaves green, narrower than in mut. *formosa*; inflorescence densely branched and many-flowered; ovaries almost sterile, producing no capsules by normal self-pollination and only shriveled capsules with few seeds by artificial pollination.....mut. *revoluta*

More extreme dwarfs, with narrowly linear leaves; inflorescence-bearing branches with broader leaves than the rest of the plant, simple, with thick-tissued, usually cleistogamous flowers which produce large normal fruits but very few viable seeds by natural self-pollination.....mut. *setacea*

The four mutations do not form a linear series showing successive degrees of reduction. Mut. *formosa* and mut. *revoluta* are very similar and might be interpreted as successive reduction stages. They differ in size and fertility, but have many morphological

characters in common. Before flowering they can be distinguished with certainty only when the environmental conditions are the same for both. Thus, mut. *revoluta* grown in a rich, moist soil is as large as mut. *formosa* grown in a dry, sandy soil. Under such conditions they might be indistinguishable until they flowered, when the latter would produce large capsules, filled with good seeds, and the former would produce few seeds or none in the shriveled ovaries. Grown under identical conditions, however, the two mutations differ at every stage of development. In some features mut. *setacea* also appears to be a reduction derivative in the same series with mut. *formosa* and mut. *revoluta*. In comparison with the latter, however, it shows a partial resumption of fertility. Its large, strong capsules are well filled, although the seeds are for the most part empty. In this characteristic, as also in its simple inflorescences and thick-tissued buds and flowers, it resembles mut. *albicans*. Mut. *setacea* is different from the other three mutations in its strong tendency to produce dimorphic foliage. The rosette leaves and young cauline plants have narrowly linear, grasslike leaves, which are succeeded above and on the inflorescence-bearing lateral branches by leaves much like those of mut. *revoluta*, which nearly always show the setiform terminal appendage. Like the latter mutation, mut. *setacea* responds greatly to environmental changes. In dry sandy soil it flowers and fruits when only 10 cm. high, but in moist loam it becomes 50 cm. high and has quite a different aspect. The comparatively broad-leaved mut. *albicans* is totally unlike the other mutations at every stage of development.

THE F₁, F₂, AND F₃ PROGENIES OF FORMA *typica*

The original wild mother plant designated as Lexington E did not give a progeny in any way peculiar when it was first grown in 1913. A casual inspection of the F₁ seedlings disclosed no mutations. The majority of the plants of this first culture were discarded as very young seedlings and only 30 were brought to maturity. These 30 plants were entirely typical. In 1914 the F₂ of the strain was found to show mass mutation. The remaining seeds of the original collection were therefore sown, in order to detect any mutability which, on account of the use of insufficiently

rigorous experimental methods, might have been overlooked the year before. The results from the new F_1 cultures of 1914 are set forth in table I.

TABLE I

ANALYSIS OF THE F_1 SEEDLING CULTURES OF LEXINGTON E

Culture	Seeds planted	Total plants	Forma typica	Mut. albicans	Mut. setacea	Mut. latifolia	Mut. graminea
2.....	200*	162	160†	○	1 (no. 35)	1 (no. 36‡)	○
3.....	199*	175	172	1 (no. 34‡)	○	○	2 (nos. 32‡ and 33‡)
4.....	203*	62	62	○	○	○	○
5.....	185*	123	123	○	○	○	○
Total	787	522	517†	1	1	1	2

* Indicates seeds from one capsule.

† 25 plants of f. typica from culture 2, grown to maturity, were uniform. The remaining plants of f. typica were discarded in the rosette stage.

‡ Indicates that the mutation was grown to maturity.

It is clear from table I that the F_1 did not point to Lexington E as a specially mutant strain. There were only 5 mutations in a progeny of 522 plants. Moreover, 2 of the 4 types obtained, mut. latifolia and mut. graminea, were common to the other strains of *O. pratincola*.

In 1914, F_2 progenies were grown from 3 plants of *O. pratincola* f. typica belonging to strain E, and the progeny of a fourth was grown in 1915. The results are summarized in table II.

The F_2 shows a decidedly greater degree of variability than the F_1 . One progeny only, that from Lexington E-5, shows mutations in excess of the number of typical plants; the other three progenies indicate a degree of mutability more comparable with that of certain derivatives of *O. Lamarckiana*, such as *O. scintillans*. The F_1 , however, was, if anything, less mutable than *O. Lamarckiana* itself. Successive generations seem to show an increasing degree of mutability. Only one F_3 progeny from f. typica has been studied. The parent belonged to the progeny of Lexington E-5, that is, it was selected from the most mutable line. The analysis of the F_3 culture is shown in table III.

The salient fact shown by the data for the F_1 , F_2 , and F_3 progenies is that the number of mutations varies inversely with the

number of seeds per capsule. The F_1 progeny, with few mutations, came from capsules with about 200 seeds. (Perhaps the capsules

TABLE II
ANALYSIS OF THE F_2 CULTURES OF LEXINGTON E, FROM 4 F_1 *f. typica* PARENTS

Parent	Culture	Seeds planted	Total plants	Forma typica†	Mut. formosa	Mut. albicans	Mut. revoluta	Mut. setacea	Other mutations	Total mutations	Percentage of mutations
Lex. E-5 . .	1	156*	131	109	0	0	3	17	2 (no. 208, <i>angustifolia</i>)	22	
" . .	2	96*	72	26	0	6	3	36	1 (no. 210, <i>chimaera</i>)	46	
" . .	3	106*	75	33	2	6	1	33	0	41	
" . .	4	75*	57	15	1	3	5	33	0	42	
" . .	5	104*	69	10	2	1	4	51	1 (no. 238, <i>gigas</i>)	59	
Total . .	1-5	537	404	194	4	15	15	172	4	210	52
Lex. E-19 . .	1	340*	270	261	0	0	4	5	0	9	
" . .	2	350*	239	224	0	0	4	11	0	15	
" . .	3	219*	150	142	0	0	4	4	0	8	
" . .	4	299*	230	219	0	0	4	7	0	11	
" . .	5	378*	143	108	0	1 (no. 67)	7	27	0	35	
Total . .	1-5	1586	1032	954	0	0	24	54	0	78	7.5
Lex. E-25 . .	1	187*	136	130	0	0	3	3	0	6	
" . .	2	225*	147	142	0	0	1	4	0	5	
" . .	3	186*	145	138	0	0	4	3	0	7	
" . .	4	180*	147	134	0	1	3	9	0	13	
" . .	5	144	72	66	0	0	1	4	1 (no. 34)	6	
Total . .	1-5	922	647	610	0	1	12	23	1	37	5.7
Lex. E-43 . .	1	410‡	275	238	0	0	1	36	0	37	
" . .	2	424‡	362	328	0	2	4	27	1 (no. 70§)	34	
Total . .	1 and 2	834	637	566	0	2	5	63	1	71	11

* Seeds from one capsule.

† Plants of *f. typica* were grown to maturity as follows: Lex. E-5, 49 plants from cultures 2, 3, 4, and 5, including all of the *typica* plants shown in figs. 1, 2, 3, 4, and 5; Lex. E-10, 18 plants from cultures 1 and 5; Lex. E-25, 23 plants from culture 5; Lex. E-43, 20 plants from culture 2. The remainder were classified in the seedling stage and discarded. The mutations were all retained and classified at maturity, except that some of the weaker specimens of mut. *setacea* died at various stages of development.

‡ Seeds of two capsules.

§ Lex. E-43-70 was a new mutation combining characters of mut. *nitida* and mut. *angustifolia*, two frequent derivatives of *O. pratincola*.

had dehisced at the apex and lost part of their seeds, as frequently happens. A normal capsule of *O. pratincola* contains 300 seeds,

more or less.) The F_2 progenies of 3 mother plants whose capsules contained an average of about 250 seeds gave about 8 per cent of mutations, the upper limit of ordinary mutability, as far as experience goes. Another F_2 progeny from a mother plant with about 110 seeds to the capsule gave over 50 per cent of mutations. Turning to the very striking F_3 progeny, we find that a mother plant

TABLE III

ANALYSIS OF F_3 CULTURES OF LEXINGTON E, FROM LEX. E-5-229, *f. typica*

Culture	Seeds planted	Total plants	Forma <i>typica</i>	Mut. <i>formosa</i>	Mut. <i>albicans</i>	Mut. <i>revoluta</i>	Mut. <i>selacea</i>	Other mutations	Total mutations	Percentage of mutations
I.....	39	30	9	0	1	1	19	0	21	70
2.....	86*	56	6	2	4	4	39	1 (<i>angustifolia</i>)	50	89.3
3.....	91*	71	17	0	3	8	43	0	54	76.1
4.....	100*	74	22	0	3	5	42	2 (<i>gigas</i> ?)	52	70.3
5.....	80*	48	20	3	3	4	18	0	28	58.3
6.....	97*	69	24	0	4	2	39	0	45	65.2
7.....	95*	51	19	0	3	1	28	0	32	62.7
8.....	104*	73	21	0	4	3	44	1 (?)	52	71.2
9.....	105*	68	30	0	3	0	35	0	38	55.9
10.....	142*	102	8	0	0	5	89	0	94	92.2
II.....	59*	39	4	0	5	2	28	0	35	89.8
12.....	79*	65	13	0	5	3	43	1 (<i>gigas</i> ?)	52	80.0
13.....	83*	65	8	1	4	6	46	0	57	87.7
14.....	85*	42	18	1	0	1	22	0	24	57.3
15.....	72*	59	19	2	6	2	30	0	40	67.8
16.....	73*	51	15	1	7	2	26	0	36	70.6
17.....	87*	73	13	0	2	5	53	0	60	82.2
Total..	1477	1036	266	10	57	54	644	5	770	74.3

* Seeds from one capsule; the entire progeny was classified from the young seedlings; 30 plants of *f. typica* and all the mutations except the weaker individuals of *mut. selacea* were retained.

with only 90 seeds to the capsule gave almost 75 per cent of mutations. It would be necessary to have much more complete data to establish any exact relationship between progressive sterility and mutability. Nevertheless, it is beyond question that the decrease in the number of seeds has gone hand in hand with the increase in mutability.

In *Oenothera pratincola*, therefore, the phenomenon which I have termed mutation *en masse* is associated with the failure of a

large number of zygotes to develop, for the number of ovules in all capsules appears to be about the same. Probably the zygotes which fail to develop into embryos represent the weaker individuals of mut. *setacea*, or perhaps some still more reduced mutation which is incapable of development. The problem, however, must be attacked by cytological methods. It is interesting to observe that the F_3 , with an average seed germination of 70 per cent, contained 75 per cent of mutations. If all the seeds had germinated, and the additional plants had all been f. *typica*, there would still have been more than 50 per cent of mutations. It seems far more likely, however, that the seeds which did not germinate were either empty or else that they were the weak mut. *setacea*.

A comparable degree of mutability to that of Lexington E is known only in the case of *O. Reynoldsii*, in which mass mutation was first described. In *O. Reynoldsii*, also, the great increase in mutability is associated with an enormously increased degree of sterility. The data in regard to the latter species will soon be published elsewhere.

A number of photographs were made to record the appearance of the mutations at various stages of growth. Figs. 1-5 show a portion of the F_2 progeny from F_1 parent Lexington E-5, recorded in table II. All of the characteristic mutations are shown, as well as several plants which became the parents of subsequent cultures. Fig. 6 shows 6 rosettes of mut. *setacea*, one of which will be found in fig. 3. Fig. 7 shows two mature plants of the same mutation, of which one is shown in fig. 5. Fig. 8 shows 4 rosettes of mut. *revoluta*, 3 of which are likewise shown in figs. 4 and 5. A mature plant is shown in fig. 9. Fig. 10 shows 6 rosettes of mut. *albicans*, 3 of which will be found in figs. 2, 3, and 4. Fig. 11 shows two caulin plants of the same form. The one on the left is just beginning to flower; the one on the right lingered in the rosette condition and would therefore have matured as a stronger plant than its sister. Rosettes of mut. *formosa* are shown in fig. 12. The main stem of the mature plant is shown in fig. 13, and the identical cross mut. *formosa* \times f. *typica* in fig. 14. Fig. 15 shows young rosettes of f. *typica* and mut. *gigas*. The *gigas* plant was the particular individual in which E. G. ARZBERGER determined the chromosome

number to be 28. For a figure showing the mature stem of *f. typica* the former article on *O. pratincola* in this journal² should be consulted.

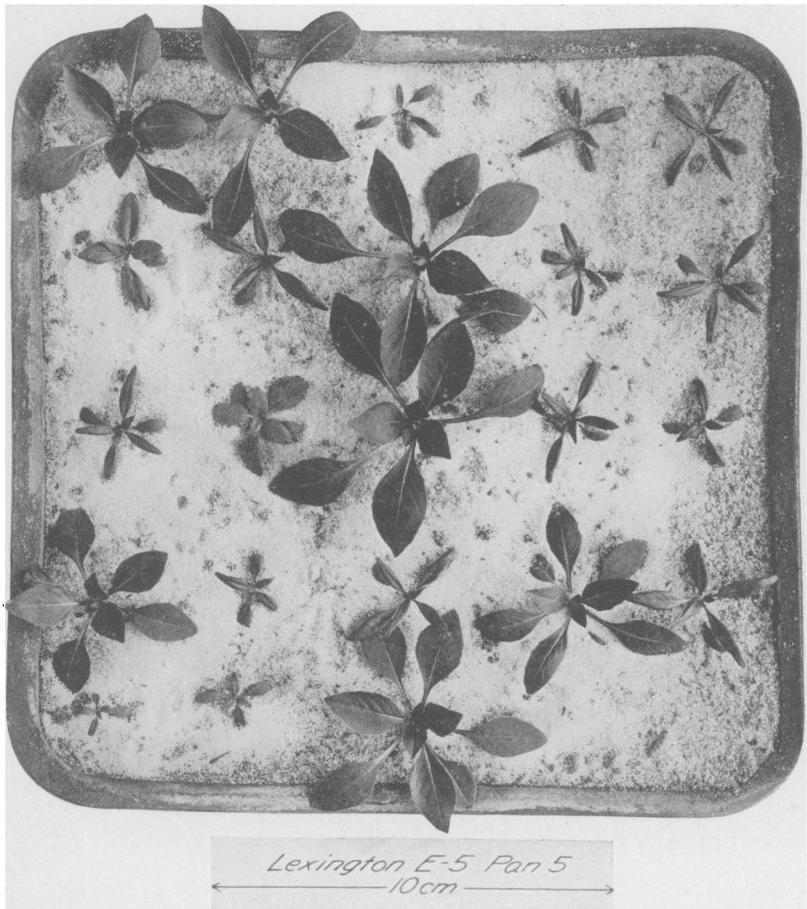


FIG. 1.—Progeny of Lexington E-5, pan 5 (part of culture 2; see table II); the pan contained 23 rosettes which were classified, most of them at maturity, as follows:

Row	1	2	3	4	5
1.....	typica	typica	setacea	setacea	setacea
2.....	albicans	setacea	typica	setacea	setacea
3.....	setacea	albicans (no. 187; see fig. 11)	typica	setacea	setacea
4.....	typica	setacea	setacea	typica	setacea
5.....	setacea	setacea	typica		

Mass mutability of the non-characteristic mutations

It has already been stated that Lexington E gives rise to certain mutations which are common to the other strains of *O. pratincola* from Lexington, and that these non-characteristic mutations, as

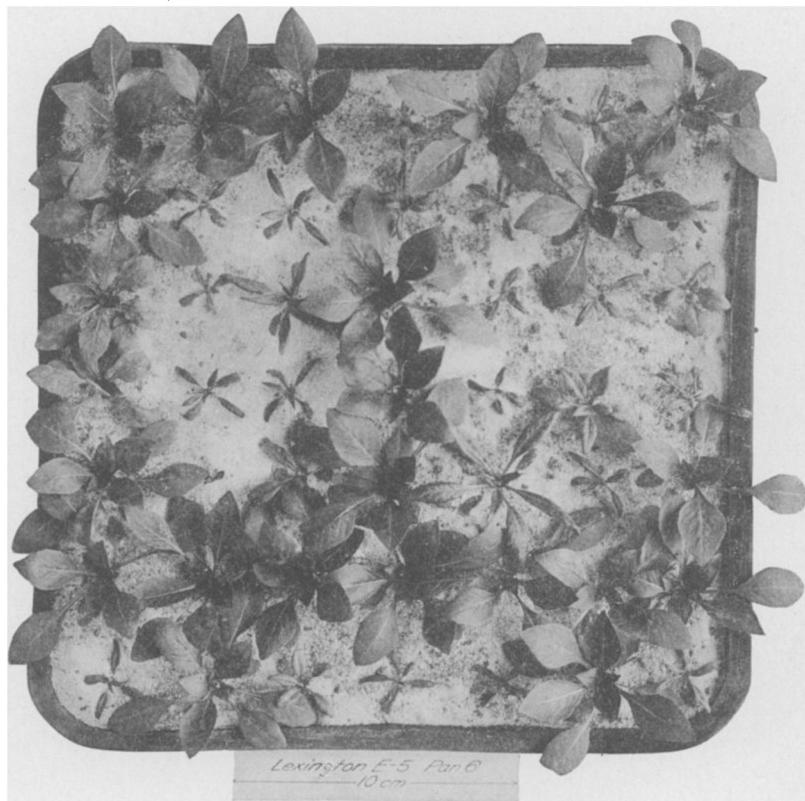


FIG. 2.—Progeny of Lexington E-5, pan 6 (part of culture 3; the remainder is shown in fig. 3; see table II); the pan contains 49 plants, classified as follows:

Row	1	2	3	4	5	6	7
1.....	typica	typica	typica	setacea	typica	setacea	typica
2.....	typica	setacea	setacea	setacea	setacea	typica	setacea
3.....	typica	setacea	setacea	typica	setacea	setacea	albicans (no. 190; see fig. 10)
4.....	typica	setacea	setacea	typica	setacea	albicans	setacea
5.....	typica	setacea	setacea	typica	formosa	setacea	typica
6.....	typica	typica	typica	typica	typica	typica	typica
7.....	setacea	typica	albicans	setacea	setacea	typica	setacea

they may be called for convenience, exhibit mass mutability superposed upon their ordinary behavior in heredity. In order to present the data in regard to this point it will be necessary to anticipate somewhat the publication of the next article of this series.

Among the mutations of *O. pratincola* which have been obtained both from Lexington E and from the strains showing only ordinary



FIG. 3.—Progeny of Lexington E-5, pan 7 (part of culture 3; the remainder is shown in fig. 2; see table II); the pan contains 26 plants, which were classified at maturity as follows:

Row	1	2	3	4	5	6
1.....	formosa	setacea	albicans (no. 191; see fig. 10)	setacea	setacea	
2.....	typica	albicans	setacea	setacea	typica	
3.....	typica	setacea	setacea	albicans	typica	
4.....	typica	setacea	typica	typica	setacea	
5.....	setacea	setacea	setacea	setacea	setacea	setacea (no. 88; see fig. 6)

mutability, two, mut. *angustifolia* and mut. *latifolia*, have been carried into an F₁ generation from parent plants derived from both sources. A third non-characteristic mutation, mut. *gigas*, has appeared in Lexington E and also, apparently, in the other strains,



FIG. 4.—Progeny of Lexington E-5, pan 8 (part of culture 4; see table II); the pan contains 49 plants, which were classified (most of them at maturity) as follows:

Row	1	2	3	4	5	6	7
1...	typica	setacea	setacea	typica	typica	setacea	setacea
2...	setacea	albicans	setacea	setacea	formosa	setacea	setacea
3...	typica	setacea	typica	revoluta (no. 203; see fig. 8)	setacea	typica	revoluta (no. 202; see fig. 8)
4...	setacea	typica	setacea	typica	typica	setacea	setacea
5...	setacea	typica	setacea	typica	setacea	albicans (no. 195; fig. 10)	setacea
6...	setacea	setacea	setacea	setacea	setacea	setacea	setacea
7...	setacea	revoluta	setacea	setacea	setacea	setacea	setacea

but no progenies have yet been grown or chromosome counts made, except in the case of one plant, belonging to the mass mutant strain.



FIG. 5.—Progeny of Lexington E-5, pan 11 (part of culture 5; see table II); the pan contains 49 plants, which were classified (most of them at maturity) as follows:

(This plant is shown in figs. 5 and 14.) All three mutations are discussed here, but full data and illustrations are reserved for a paper entitled "Certain mutations and hybrids of *Oenothera pratincola*," to appear later in this journal.

Mut. *angustifolia*.—It has been found that mut. *angustifolia* from ordinary strains gives no descendants resembling itself; aside from the usual small proportion of other mutational types, the progeny consisting of f. *typica* only. The variation, although striking and entirely discontinuous, appears to be somatic. In this connection it is interesting to note that a perfect branch of f. *typica* has been observed as a bud sport on mut. *angustifolia*. As would be expected, mut. *angustifolia* crossed reciprocally with f. *typica* gives f. *typica* together with the usual few mutations. The hereditary behavior may be stated:

mut. *angustifolia* × mut. *angustifolia* → f. *typica*

mut. *angustifolia* × f. *typica* → f. *typica*

f. *typica* × mut. *angustifolia* → f. *typica*

The behavior of mut. *angustifolia* from Lexington E is most remarkable. The parent plant was a sister of the *typica* plant whose progeny is analyzed in table III, but the degree of mutability proved to be much more extreme than in the case of the *typica* sister. Only two plants in the progeny, out of a total of 505, were f. *typica*; the other 503 plants, 99.6 per cent of the progeny, were mutations belonging to the group characteristic of Lexington E. The results are summarized in table IV.

The cross mut. *angustifolia* × f. *typica* and the reciprocal gave respectively 100 per cent and 91.5 per cent of mutations. By comparison with table III it will be seen that each of the reciprocal crosses tends to show the same degree of mutability as the female parent. To be sure, there would seem to be a considerable discrepancy between 74.3 per cent, representing the mutability of f. *typica*, and 91.5 per cent, representing the mutability of f. *typica* × mut. *angustifolia*. No significance can be urged for this discrepancy, however, when we consider that one of the cultures from a single capsule of f. *typica* contained 92.2 per cent of mutations among 102 plants, as compared with 91.5 per cent of mutations

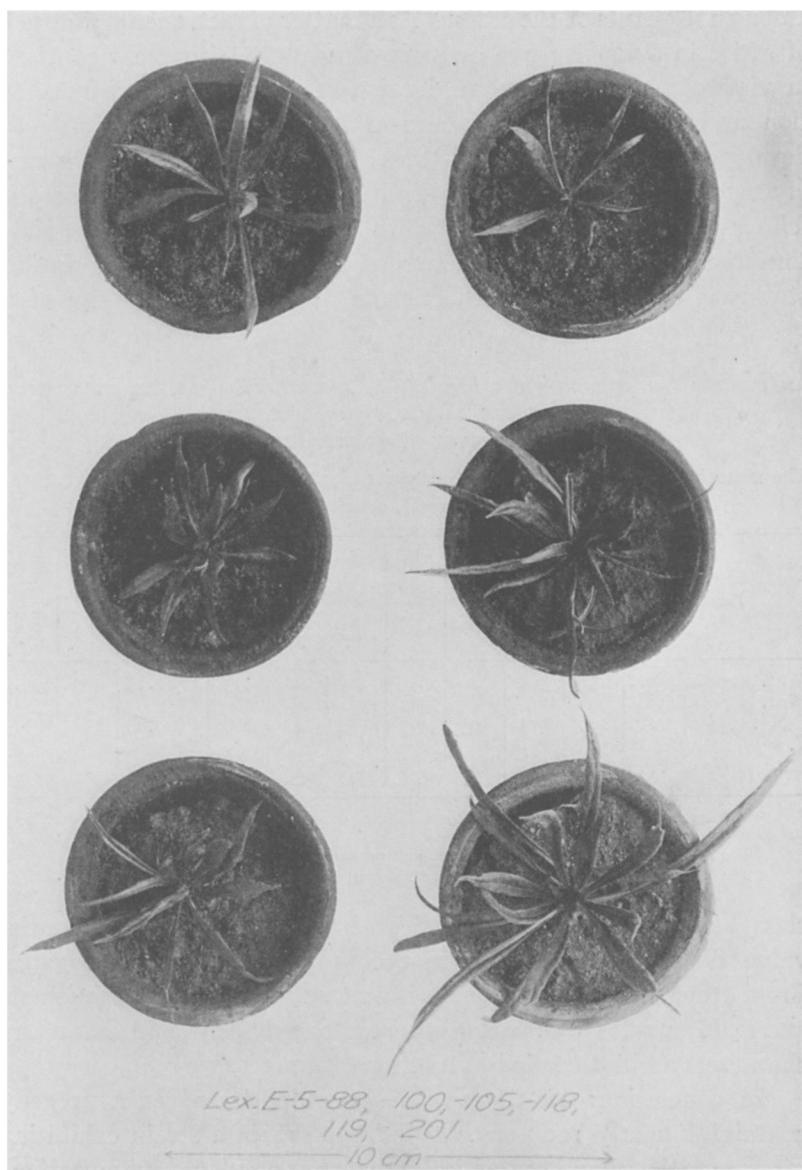


FIG. 6.—*Mut. setacea*: 6 rosettes of the F_2 progeny of *f. typica*, from F_1 parent Lexington E-5; the plant in the upper left-hand corner, Lexington E-5-88, is shown also in fig. 3.

among 118 plants of the cross. As a matter of fact, the significance of ratios in *Oenothera* can be maintained only with great caution, in view of the enormous elimination of gametes during maturation and the subsequent failure of large classes of zygotes to develop. Nevertheless, the absence or almost complete absence of a strong zygote such as f. *typica* in the progenies of mut. *angustifolia* and mut. *angustifolia* × f. *typica* is strong evidence for the view that the composition of the progeny among the mass mutating strains is conditioned by the female gametes. The failure of a

TABLE IV

ANALYSIS OF F₁ CULTURES OF MUT. *angustifolia*, LEXINGTON E-5-208, SELF-POLLINATED AND RECIPROCALLY CROSSED WITH F. *typica*, LEXINGTON E-5-229 (THE PLANT WHOSE PROGENY IS ANALYZED IN TABLE III)

The mutation was a sister plant of the *typica* plant with which it was crossed; for position in pedigree see table II, culture 1 from Lexington E-5

Parent	Seeds planted	Total plants	Forma <i>typica</i>	Mut. <i>formosa</i>	Mut. <i>albicans</i>	Mut. <i>revoluta</i>	Mut. <i>setacea</i>	Other mutations	Total mutations	Percentage of mutations
Mut. <i>angustifolia</i> ..	651*	505	2	4	2	21	475	1 (no. 1)	503	99.6
Mut. <i>angustifolia</i> ·×f. <i>typica</i>	199†	173	0	0	0	4	168	1 (no. 1)	173	100
F. <i>typica</i> × mut. <i>angustifolia</i>	182‡	118	10	0	1	4	99	4	108	91.5

* The 651 seeds were from 11 capsules, containing respectively 51, 75, 53, 62, 44, 59, 82, 101, 46, 33, and 45 seeds.

† The 199 seeds were from 3 capsules, containing respectively 73, 47, and 79 seeds.

‡ The 182 seeds were from 2 capsules, containing respectively 79 and 103 seeds.

class of strong zygotes to appear has much greater evidential value than any fluctuation in the proportion of weak zygotes. From other sources the evidence is unusually strong that the female and male gametes of *O. pratincola* are not equivalent, and that many characters are not carried by the male gametes.

In conclusion: mut. *angustifolia* ordinarily gives a progeny containing nearly 100 per cent of f. *typica*; in a strain exhibiting mass mutation many of the *typica* plants are replaced by mutations of the characteristic group. Presumably other individuals of mut. *angustifolia* could be found which would be less mutable than the one tested, just as different individuals of f. *typica* show widely

varying degrees of mutability. The progenies of crosses indicate that mass mutability is conditioned by the female gametes.

Mut. *latifolia*.—In contrast with mut. *angustifolia*, mut. *latifolia* reproduces itself in part of its progeny. Its descendants include roughly 50 per cent f. *typica* and 50 per cent mut. *latifolia*, the proportion varying within rather wide limits. Moreover, mut. *latifolia* gives progenies of the same type whether self-pollinated or



FIG. 7.—Mut. *setacea*: 2 mature plants from the F_2 progeny of f. *typica*, from F_1 parent Lexington E-5; the right-hand plant, Lexington E-5-164, is shown also in fig. 5; note particularly the dimorphic foliage.

cross-pollinated with f. *typica*. The reciprocal cross, with f. *typica* as the pistillate parent, consists only of f. *typica*, aside from the usual low proportion of mutations, among which mut. *latifolia* may or may not happen to occur. These relations are as follows:

$$\begin{aligned} \text{mut. } &\text{latifolia} \times \text{mut. } \text{latifolia} \rightarrow \text{f. } \text{typica} + \text{mut. } \text{latifolia} \\ \text{mut. } &\text{latifolia} \times \text{f. } \text{typica} \rightarrow \text{f. } \text{typica} + \text{mut. } \text{latifolia} \\ \text{f. } &\text{typica} \times \text{mut. } \text{latifolia} \rightarrow \text{f. } \text{typica} \end{aligned}$$

The type of heredity here exemplified is shown by several mutations from *O. Lamarckiana*. *O. lata* DeVries provides the classic case. The heredity of *O. scintillans* DeVries and *O. oblonga*

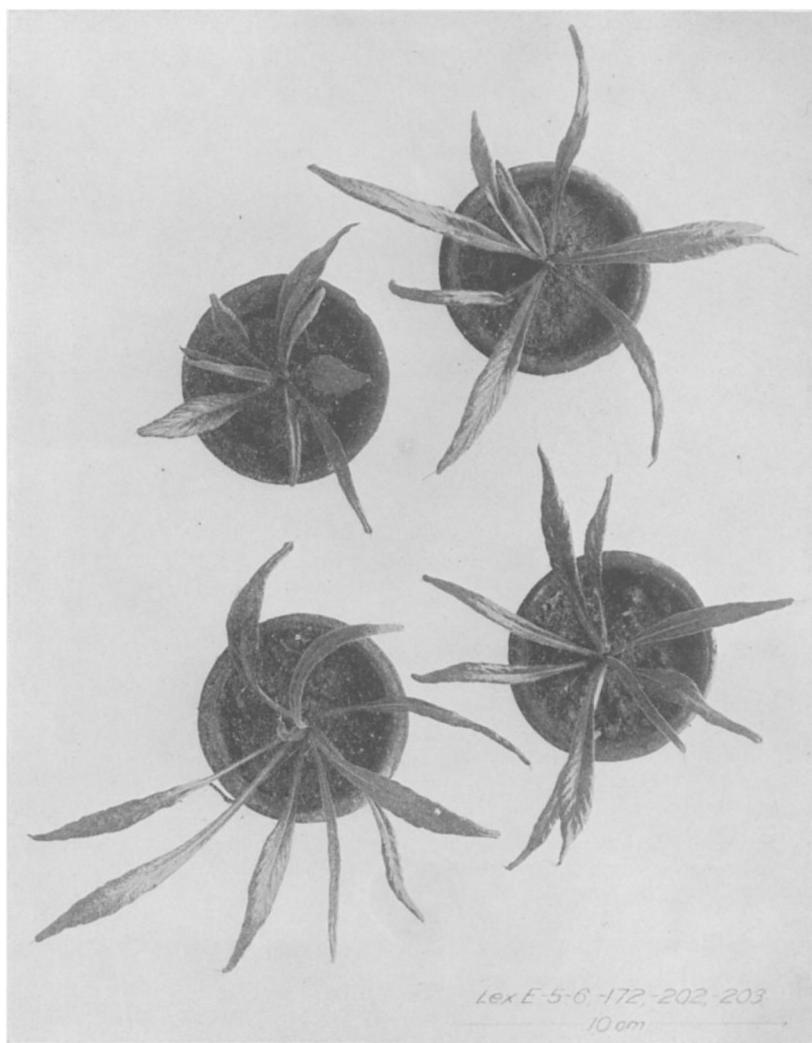


FIG. 8.—Mut. *revoluta*: 4 rosettes of the F₂ progeny of f. *typica*, from F₁ parent Lexington E-5; the upper right-hand plant, Lexington E-5-172, will be found in fig. 5; the two lower plants, nos. E-5-202 and 203, will be found in fig. 4.

DeVries is in essentials the same.⁷ Another case is provided by *O. stenomeres* mut. *lasioptala*.⁸ HERIBERT-NILSSON⁹ has recently described several new mutations from *O. Lamarckiana* ("heterogame Kombinant" *dependens*, *undulata*, *stricta*, etc.) which probably show the typical *lata* type of inheritance, although he erroneously concludes that the repeated segregation of *O. Lamarckiana* from these mutations in each generation is due to the existence of two types of functioning gametes on the male rather than on the female side.

It must not be inferred from the similarity of the names that mut. *latifolia* is a parallel variation to *O. lata* DeVries. Such is not the case. Its characters are quite different. Both mut. *latifolia* and mut. *angustifolia* will be described and illustrated in a future article.

As in the case of mut. *angustifolia*, the progeny of mut. *latifolia* from the mass mutating strain contained the expected types, f. *typica* and mut. *latifolia*, together with the characteristic mutations. The latter did not show differences among themselves which would enable one to classify them as modified *typica* or modified *latifolia*, as the case might be. The mother plant belonged to the F₁ generation from Lexington E, and showed about the same degree of mutability as the *typica* sister plant, Lexington E-5 (see table II). The data for mut. *latifolia* are summarized in table V.

Mut. *gigas*.—E. G. ARZBERGER's discovery that this mutation has 28 chromosomes has already been announced.¹⁰ The count has been made only in one plant, Lexington E-5-238 (figs. 5 and 14), belonging to the mass mutant strain. An apparently identical mutation in one of the other strains has appeared this summer (1915), but its heredity is unknown. Mut. *gigas* is treated, therefore, as a non-characteristic mutation. Only 196 seeds were

⁷ For the latest treatment of these mutations see DEVRIES, Gruppenweise Artbildung. pp. 244-267.

⁸ BARTLETT, H. H., The mutations of *Oenothera stenomeres*. Amer. Jour. Bot. 2: 100-109. 1915.

⁹ HERIBERT-NILSSON, N., Die Spaltungserscheinungen der *Oenothera Lamarckiana*. Lunds Universitets Arsskrift. N.F. Avd. 2. 12: no. 1. pp. 132. 1915.

¹⁰ BARTLETT, H. H., The experimental study of genetic relationships. Amer. Jour. Bot. 2:132-155. 1915 (see p. 143).

obtained from 15 capsules of the primary mutation, Lexington E-5-238. The progeny consisted of 25 plants, only 16 of which survived transplanting from the seed pan. None of the progeny resembled the parent. All were extreme dwarfs which resembled, but were not identical with, mut. *revoluta* and mut. *setacea*. They differed mainly in the thicker leaves, which in 4 plants were narrow but not markedly revolute. Although a very nondescript lot, differing much among themselves, 5 most resembled mut. *revoluta*, and 7 mut. *setacea*. The result of this culture might almost have been predicted. The mass mutability was inherited by mut. *gigas* from f. *typica*. In view of the dependence of the *gigas* characters upon

TABLE V

ANALYSIS OF AN F₁ CULTURE FROM SELF-POLLINATED MUT. *latifolia*, LEXINGTON E-36
The parent plant belonged to the F₁ from Lexington E, f. *typica*; see table I, culture 2,
for position in pedigree

Parent	Seeds planted	Total plants	Forma <i>typica</i>	Mut. <i>latifolia</i>	Mut. <i>albicans</i>	Mut. <i>revoluta</i>	Mut. <i>setacea</i>	Other mutations	Total mutations†	Percentage of mutations‡
Lex. E-36, mut. <i>latifolia</i>	375*	182	95	48	5	2	29	3†	87	47.8

* Seeds from 7 capsules, containing respectively 54, 72, 49, 30, 38, 70, and 62 seeds.

† Nos. 32 and 43, a new mutation; no. 51 mut. *gigas* (?), morphologically identical with Lexington E-5-238 which had 28 chromosomes; see table II, culture 5 from Lexington E-5, for position of latter plant in pedigree.

‡ Excluding, of course, mut. *latifolia*.

the double complement of chromosomes, which would in general be handed on to any secondary mutations, it follows that the mutations occurring *en masse* would not be identical with those from f. *typica*. Furthermore, chance irregularities in chromosome distribution might increase the polymorphism of the progeny. In such a highly modified germ plasm irregularities would be expected.

The cross mut. *gigas* × f. *typica* yielded 160 seeds in a single capsule, of which 10 germinated. The plants were all extreme dwarfs, of the most nondescript nature, hardly any two alike. All had thick leaves, some plane, others revolute. No mutation of

f. typica could be identified among them. The reciprocal cross yielded no seeds.

Inheritance and mutability of the characteristic mutations

Of the group of characteristic mutations, including mut. *formosa*, mut. *albicans*, mut. *revoluta*, and mut. *setacea*, only the first is both normally fertile and vigorous. The second is vigorous, but produces few good seeds. The third is almost sterile, and the fourth is not only difficult to cultivate, but like mut. *albicans* gives very few good seeds. All of the forms were self-pollinated and reciprocally crossed with *f. typica* in 1914, but, except in the case of mut. *formosa*, the resulting *F₁* cultures were very fragmentary or entire failures. The other three forms bloomed in September, when only a few weak, belated flowers of *f. typica* were available for the crosses. The results of the cultures are summarized in table VI.

Mut. *formosa*.—The entirely satisfactory cultures of this form show that it is constant in the sense that it gives no reverions to *f. typica* in its progeny. Moreover, there is no



FIG. 9.—Mut. *revoluta*: a mature plant, Lexington E-19-21 (for position in pedigree see table II).

TABLE VI

ANALYSIS OF F_1 CULTURES IN THE GROUP OF MUTATIONS CHARACTERISTIC OF MASS MUTABILITY

Parentage culture		Seeds planted	Total plants	<i>Forma typica</i>	Mut. <i>formosa</i>	Mut. <i>albicans</i>	Mut. <i>revoluta</i>	Mut. <i>setacea</i>	Other mutations	Total mutations
Mut. <i>formosa</i> Lex. E-5-199	1.....	244*	196	○	171	○	1	24	○	25
	2.....	269*	163	○	137	○	○	26	○	26
	3.....	201*	177	○	149	○	2	26	○	28
	4.....	216*	174	○	130	1	○	43	○	44
	5.....	217*	193	○	150	○	1	42	○	43
	6.....	224*	179	○	146	○	○	33	○	33
	Total.....	1-6	1371	○	883	1	4	194	○	199
Mut. <i>formosa</i> Lex. E-5-199	×	365†	309	○	218	○	○	91	○	91
<i>f. typica</i> Lex. E-5-217										
Mut. <i>formosa</i> Lex. E-5-206		177‡	146	○	130	2	○	14	○	16
Mut. <i>formosa</i> Lex. E-5-206	×	233§	177	○	151	○	3	23	○	26
<i>f. typica</i> Lex. E-5-229										
<i>F. typica</i> Lex. E-5-229	×	246	133	7	○	1	○	121	4	126
mut. <i>formosa</i> Lex. E-5-206										
Mut. <i>albicans</i> Lex. E-19-67 (seeds of 4 capsules)....		386	265	○	○	36	3	226	○	229
Mut. <i>albicans</i> Lex. E-5-182 (seeds of 4 capsules)....		173	69	○	○	7	3	59	○	62
<i>F. typica</i> Lex. E-5-229	×	22*	14	1	○	○	1	12	○	13
mut. <i>albicans</i> Lex. E-5-182										
Mut. <i>revoluta</i> Lex. E-5-190 (seeds of 14 capsules)....		85	23	○	○	1	17	5	○	6
Mut. <i>setacea</i> Lex. E-5-17 (seeds of 4 capsules)....		625	140	○	○	○	○	140	○	○
Mut. <i>setacea</i> Lex. E-5-20 (seeds of 16 capsules)....		1997	8	○	○	○	○	8	○	○
Mut. <i>setacea</i> Lex. E-5-66 ..		114*	31	○	○	○	○	31	○	○
Mut. <i>setacea</i> Lex. E-5-135 (seeds of 3 capsules)....		463	14	○	○	○	○	14	○	○

* Seeds from one capsule.

† Seeds from 2 capsules; 215+150.

‡ Seeds from 2 capsules; 48+129.

§ Seeds from 2 capsules; 64+169.

|| Seeds from 2 capsules; 115+131.

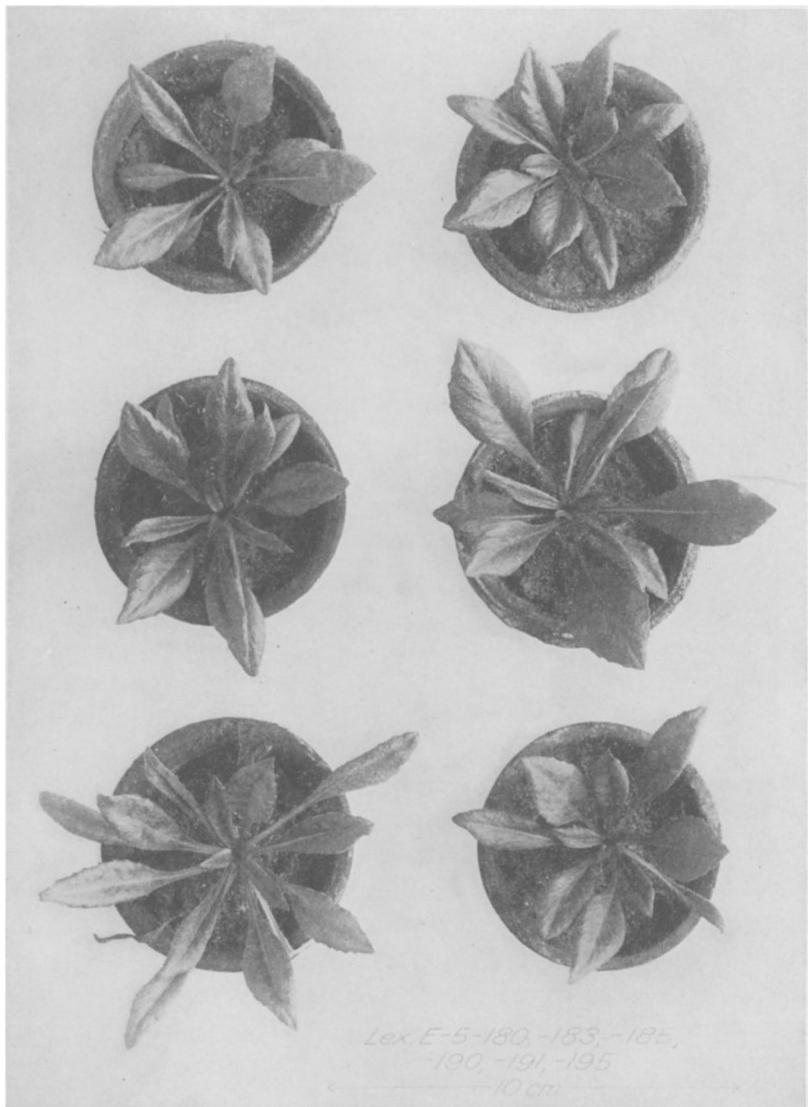


FIG. 10.—*Mut. albicans*: 6 rosettes of the F_2 progeny of *f. typica*, from F_1 parent plant Lexington E-5; the right-hand plant in the middle row, Lexington E-5-190, will be found in fig. 2; the two plants in the lower row, E-5-191 (left) and 195 (right), will be found respectively in figs. 3 and 4.

difference between the progenies resulting from self-pollination and those resulting from pollination with *f. typica*. In other words, mut. *formosa* is dominant over *f. typica* if it enters the cross as a female gamete, but is not even dominant over the weak mut. *setacea* when the *formosa* gamete is male. The scheme of heredity is:

$$\text{mut. } formosa \times \text{mut. } formosa \rightarrow \text{mut. } formosa$$

$$\text{mut. } formosa \times f. typica \rightarrow \text{mut. } formosa$$

$$f. typica \times \text{mut. } formosa \rightarrow f. typica$$

It would have been instructive to cross mut. *formosa* reciprocally with *f. typica* from a non-mass mutant strain. (Such crosses have been made this year and will be grown next year.) From the data at hand, concerning only crosses within the mass mutant strain, it appears clear that the external features of all the characteristic mutations are determined by the female gametes. The female and male gametes are not equivalent. Thus, the progeny obtained from *f. typica*, Lex. E-5-229, by pollination with mut. *formosa* is not significantly different from the progeny obtained by self-pollination (cf. tables III and VI). The characteristic mutations occur with their usual frequency regardless of which pollen is used. We know that this particular individual of *f. typica* gave about 1 per cent mut. *formosa* when grown in large cultures from self-pollinated seeds. That pollination with pollen of mut. *formosa* does not increase the proportion of this mutation in the progeny is strikingly shown by the absence of even a single individual among the 133 plants of the cross. In a culture of this size from self-pollinated seed the chances are about even that an individual of mut. *formosa*, with a frequency of 1 per cent, would or would not turn up. If the use of *formosa* pollen had appreciably increased the frequency of this form in the progeny, a culture of 133 plants might have been expected to show it. The results can be interpreted in only one way, that is, the female gamete carries all the factors which determine the visible characters of the several forms, not only of the 4 mutations, but of *f. typica* as well.

Both parent plants of mut. *formosa* showed a high degree of mutability themselves, and gave rise to the other 3 characteristic

mutations. As in the case of progenies from *f. typica*, mut. *angustifolia*, and mut. *latifolia*, the predominating form among the mutations was mut. *setacea*.



FIG. 11.—Mut. *albicans*: 2 cauline plants, Lexington E-5-196 (left) and 187 (right), from the F₂ progeny of *f. typica*; no. 187 is shown also in fig. 1.

Mut. *albicans*.—This mutation reproduces itself in only a small proportion of its progeny, but can be said to come true in the sense

that it gives no reversions to *f. typica*. All of the aberrant plants in the cultures, both from self-pollination and from pollination with *f. typica*, are mutations belonging to the characteristic group. As in the case of *mut. formosa*, most of the secondary mutations were *mut. setacea*.

The small culture of *f. typica* \times *mut. albicans* emphasizes the fact that the composition of the culture is conditioned by the female

gamete. As in the case of the analogous cross *f. typica* \times *mut. formosa*, the progeny is just what we should expect from self-pollination of the *typica* parent.

Mut. revoluta.—Only one small progeny was obtained from this nearly sterile mutation. It showed that the form reproduces itself except for throwing other mutations of the characteristic group. None of the crosses made with *mut. revoluta* were successful, but there can be little doubt, from collateral evidence, that *mut. revoluta*, as well as *mut. albicans*, follows the same type of inheritance as *mut. formosa*.

Mut. setacea.—So far as can be determined, this form comes entirely true from seed, and represents the most

FIG. 12.—*Mut. formosa*: 2 rosettes, Lexington E-5-206 and 207, from the F_2 progeny of *f. typica*; both are shown in fig. 5.

extreme modification which can take place in the direction followed by the group of characteristic mutations. Although the crosses with *f. typica* have so far not been successful, it is probable that this extreme reduction phase would also be dominant when introduced into the cross as the female gamete.



The numerical data for mut. *setacea* in all cultures have had to be based largely on the determination of very young plants, for many weak plants do not succeed in forming new roots after being transplanted. There is no difficulty in growing to maturity practically every individual of mut. *formosa* that germinates, and most of those of mut. *albicans* and mut. *revoluta*. It is the rule rather than the exception, however, to lose three-fourths or more of the *setacea* plants. They show some variation among themselves which may possibly indicate that mut. *setacea* is itself mutable and that more than one type is covered by this name. If so, only one type survives in the part of the cultures which reaches maturity.

The phenomenon of mass mutation

From the results of the crosses between f. *typica* and muts. *formosa* and *albicans*, as well as from the insignificant variation in the composition of cultures showing mass mutation regardless of the source of the pollen, it appears clear that the factors responsible for the mutational characters are carried in the



FIG. 13.—Mut. *formosa* (Lexington E-5-206-51): the setiform leaf appendages show very clearly; the position of the plant in the pedigree may be determined from table VI.

female gametes. So far, there is no evidence that the pollen of any of the characteristic mutations differs from that of *f. typica*.



FIG. 14.—Mut. *formosa* × *f. typica* (Lexington E-5-206 × E-5-229, one of the *F₁* progeny): this cross is identical with mut. *formosa* itself (cf. fig. 13); the constitution of the *F₁* progeny is given in table VI; the progenies resulting from self-pollination of the parent plants are recorded in tables III and VI.

It follows that mass mutation in *O. pratincola* must be due to the wholesale modification of female gametes. The relations have not been worked out in the case of *O. Reynoldsii*, which also shows mass mutability.

There can be no doubt that mass mutation is not Mendelian segregation, although the two phenomena have points of resemblance. HERIBERT-NILSSON's hypothesis to account for the mutability of *O. Lamarckiana* depends upon the segregation of plural factors for the same character, and involves such complications as the elimination of all zygotes which are homozygous with regard to the presence of any of the numerous plural factors. Needless to say, he has also relied upon the doctrine of the equivalence of male and female gametes. His

last paper bears evidence that his faith in the equivalence of gametes is beginning to waver, although he has formerly trusted so

implicitly that he has made crosses only one way. If he had studied the reciprocals of his crosses it is safe to assume that he would never have advanced his Mendelian explanation of mutability. As far as his results extend, his derivatives of *O. Lamarckiana* fall, for the most part, into two classes, which conform in hereditary behavior to the two main classes of mutations which have been obtained from *O. pratincola*.

Class I.—The mutation breeds true, in the sense that it gives no reverions to the parent form. The reciprocal crosses with the parent species are matroclinic. The progeny conforms to the type which supplies the female gamete.

Class II.—The mutation gives a progeny consisting of the parental and mutational types in greatly varying proportions. The progenies from reciprocal crosses are mixed if the mutation supplies the female gametes, but consist of the parental type only if the mutation supplies the male gamete.

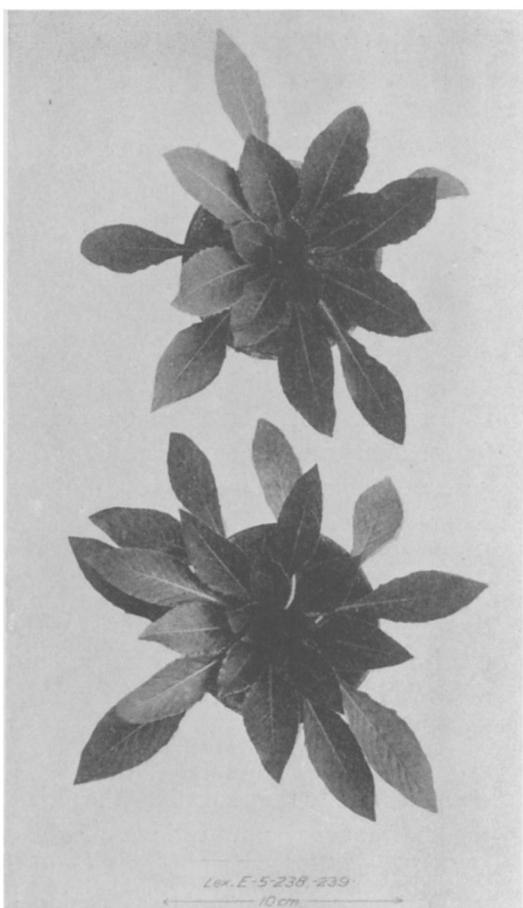


FIG. 15.—*Mut. gigas* (above) and *f. typica* (below): rosettes from the F_1 progeny of *f. typica*; the rosette of *mut. gigas*, Lexington E-5-238, had a darker color and more conspicuous pubescence than the sister plant of *f. typica*, but the difference does not appear in the photograph; both plants are shown in fig. 5.

Several mutations of each class have been studied by the writer in more or less detail, and the results will soon be published. As already announced,¹¹ the interesting mut. *nummularia* belongs to class I, as do also all of the mutations characteristic of Lexington E. Mut. *latifolia* is a typical member of class II. There are mutations, of course, which show neither type of behavior, but they need not be involved in the present discussion.

HERIBERT-NILSSON's hypothesis demands the recessiveness of mutations of class I, regardless of which way they are crossed with the parent. This condition is not fulfilled. It demands that the female gametes of the mutations of class II should be of one kind, and the pollen of two kinds. Neither is this condition fulfilled. His hypothesis makes no provision for the appearance of mutations in excess of one-third of the progeny. In this respect it is quite inadequate. On Mendelian grounds it is as difficult to account for too many mutations as for too few. His assumption is that after a homozygous and recessive condition has been attained in *O. Lamarckiana*, except for one of the plural factors which produce the *Lamarckiana* phaenotype, monohybrid splitting will take place. The one-fourth of dominant homozygotes will be eliminated, and therefore the progeny will consist of heterozygotes and recessives (mutations) in a 2:1 ratio. He has not attempted to explain how more than one-third of a progeny can consist of mutations, although he states in a vague and general way that the discovery of highly mutable strains is an argument in favor of his thesis. Nothing, he says, has made the mutation phenomena appear so exceptional as the low frequency of mutations. In his opinion, the high mutability of *O. Reynoldsii* has rendered the mutation fiction an absurdity.

Further comment on this opinion is rendered unnecessary by the serious discrepancies between HERIBERT-NILSSON's hypothesis and the facts. It can do no harm to point out, however, that even if mutations appeared through the operation of Mendelian segregation, as no one denies may sometimes be the case, it is still necessary to account for the origin of heterozygosis in the parent strain. The writer believes that mutations may often appear as a result of segregation, but that the antecedent heterozygosis has its origin in a mutative change. To attempt to account for the hetero-

¹¹ Amer. Jour. Bot. 2:146. 1915.

zygosis by hybridization leads to such absurdities as the denial that new forms have ever originated except by hybridization and recombination.

It is perhaps unwise to hazard even a guess at the nature of the modification of the female gametes which results in mass mutation. At one time the writer was inclined to believe that the modification had involved the cytoplasm rather than the nucleus, and that cytoplasmic inheritance might account for the matroclinic crosses. However, there are now adequate data at hand to show that similar matroclinic crosses in other cases cannot be explained by cytoplasmic inheritance. The reason for discarding this hypothesis will be explained in a future paper, since it involves data which cannot be touched upon here.

Mendelian expectations require that the largest class in a progeny showing mutation shall consist of the parent phaenotype. No explanation of the high mutability of mass mutating strains can be accepted which requires the elimination of zygotes of this phaenotype, which according to all other experience are strong and viable. If a deficiency in any class of zygotes were to be expected in a mass mutant strain, it would be the class of weakest mutations; in the case of *O. pratincola*, for example, it would be mut. *setacea*. Yet this mutation is the very one which occurs in the largest numbers.

Mass mutation is neither more nor less easily explained than ordinary mutation. It seems to be due to sudden mutative transformations of certain female gametes, and to be apparent in the zygotes without the necessity of subsequent segregation because of the fact that the factors involved have no counterparts in the male gametes. There is no real distinction between mass mutation and ordinary mutation except that in the former type large numbers of gametes may be simultaneously affected, whereas in the latter only a few are affected.

Summary and conclusions

1. Mass mutation consists in the production of unexpectedly large numbers of mutations, in some cases amounting to 100 per cent of the progeny.

2. The phenomenon is known in two species of *Oenothera*: *O. Reynoldsii*, in which it was first described, and *O. pratincola*, the subject of this paper.

3. It cannot be explained by HERIBERT-NILSSON'S Mendelian hypothesis.

4. The mutations of the mass mutant strain of *O. pratincola* are:
(A) common to other strains of the species; the non-characteristic mutations are not produced in unexpected numbers and show mass mutability superposed upon their ordinary behavior in heredity;
(B) characteristic of the mass mutant strain.

5. The characteristic mutations are constant in that they do not throw the type form of the species, but, except in the case of the most reduced member of the group, are themselves highly mutable.

6. As far as tested, the characteristic mutations adhere to the following scheme of inheritance:

mutation \times mutation \rightarrow mutation

mutation \times parent \rightarrow mutation

parent \times mutation \rightarrow parent

7. They belong to a group with certain structural characters in common, but do not seem to form a linear reduction series.

8. They seem to result from the mutative modification in the female gametes of factors which have no counterparts in the male gametes.

9. Mass mutation is associated with a high degree of sterility, which manifests itself in the production of a greatly reduced number of seeds or in the production of many empty seeds.